Published in "Developmental Psychobiology 59(2): 185–196, 2017"
which should be cited to refer to this work.

The "when" and the "where" of single-trial allocentric spatial memory performance in young children: Insights into the development of episodic memory

Farfalla Ribordy Lambert[1] | **Pierre Lavenex**[1,2] | **Pamela Banta Lavenex**[2]

[1] Laboratory of Brain and Cognitive Development, Department of Medicine, Fribourg Center for Cognition, University of Fribourg, Fribourg, Switzerland

[2] Laboratory for Experimental Research on Behavior, Institute of Psychology, University of Lausanne, Lausanne, Switzerland

Correspondence
Pamela Banta Lavenex, Laboratory for Experimental Research on Behavior, Institute of Psychology, University of Lausanne, 1015 Lausanne, Switzerland.
Email: pamela.bantalavenex@unil.ch

Funding information
Swiss National Science Foundation, Grant numbers: PMPDP3-122844, PMPDP3-128996

Abstract

Allocentric spatial memory, "where" with respect to the surrounding environment, is one of the three fundamental components of episodic memory: what, where, when. Whereas basic allocentric spatial memory abilities are reliably observed in children after 2 years of age, coinciding with the offset of infantile amnesia, the resolution of allocentric spatial memory acquired over repeated trials improves from 2 to 4 years of age. Here, we first show that single-trial allocentric spatial memory performance improves in children from 3.5 to 7 years of age, during the typical period of childhood amnesia. Second, we show that large individual variation exists in children's performance at this age. Third, and most importantly, we show that improvements in single-trial allocentric spatial memory performance are due to an increasing ability to spatially and temporally separate locations and events. Such improvements in spatial and temporal processing abilities may contribute to the gradual offset of childhood amnesia.

KEYWORDS
development, early, learning, memory, spatial, temporal

1 | INTRODUCTION

Episodic memory enables individuals to remember events that occurred in unique spatiotemporal contexts, that is, in particular places at particular times (Tulving, 2002). Episodic memory is conceptualized as integrating three types of information: (1) "what," specifically the event or what happened to whom; (2) "where," the location of the event in space; and (3) "when," the occurrence of the event in a relative temporal framework (Nyberg et al., 1996). As episodes occur only once, single-trial learning of "what," "where," and "when" information is considered a pre-requisite for the establishment of long-term episodic memory (Schwartz, Colon, Sanchez, Rodriguez, & Evans, 2002).

Episodic memory is not a faculty that we are born with but rather one that emerges during early childhood. Infantile amnesia is the term used to describe the fact that as adults we have essentially no episodic memories from the first 2–3 years of our life, whereas childhood amnesia describes the fact that as adults we have fewer episodic memories from 3 to 7 years of age than would be expected based on normal forgetting alone (Bauer, 2007; Jack & Hayne, 2010; Newcombe, Lloyd, & Ratliff, 2007; Rubin, 2000). Although it is clear that children's episodic recall is far from adultlike, which specific aspects are lacking is not yet clear. Recent studies attempted to evaluate children's episodic memory in the laboratory, or in the child's own home, using paradigms designed to tease apart the "what," "where," and "when" components of episodic memory acquired via experimenter-defined events (Bauer et al., 2012; Hayne & Imuta, 2011; Newcombe, Balcomb, Ferrara, Hansen, & Koski, 2014). Other studies analyzed the developmental trajectories of the "what," "where," or "when" components separately, and thus independently of episodic events, in order to identify age-specific deficiencies in the individual components of episodic memories, which may be responsible for hindering the successful encoding, storage, and recall of episodic memories (Lee, Wendelken, Bunge, & Ghetti, 2016; Ribordy, Jabes, Banta Lavenex, & Lavenex, 2013; Ribordy Lambert, Lavenex, & Banta Lavenex, 2015).

"Where" an event took place is dependent on allocentric spatial memory, the memory for locations coded in relation to objects

comprising the surrounding environment (Burgess, 2002; Hoscheidt, Nadel, Payne, & Ryan, 2010). Similar to a stool missing one of its three legs, episodic memories are not viable without allocentric spatial information. Both episodic and allocentric spatial memory are dependent on the hippocampal formation in humans (Banta Lavenex, Colombo, Ribordy Lambert, & Lavenex, 2014; Scoville & Milner, 1957; Zola-Morgan, Squire, & Amaral, 1986), and episodic recall that includes retrieving spatial context activates the hippocampal formation (Hoscheidt et al., 2010). In addition, episodic and allocentric spatial memory follow the same developmental time course (Lavenex & Banta Lavenex, 2013). The offset of infantile amnesia, when children become capable of long-term encoding of some, albeit few, episodic memories, occurs around 2 years of age (Newcombe et al., 2007; Rubin, 2000). Similarly, basic allocentric spatial memory abilities are reliably observed in children after 2 years of age (Newcombe, Huttenlocher, Bullock Drummey, & Wiley, 1998; Ribordy et al., 2013, Ribordy Lambert et al., 2015).

In a series of experiments by Ribordy et al. (2013) and Ribordy Lambert et al. (2015), children were asked to find rewards hidden beneath cups in an open-field arena, over repeated trials. The simplest version of this task required children to learn and remember one rewarded location among four potentially rewarded locations. Whereas 20- to 24-month-old children could discriminate the rewarded location in the presence of a local cue, only children 24 months of age and older were capable of performing above chance when required to use an allocentric spatial representation to define the goal location. These findings confirmed earlier findings by Newcombe and co-workers showing that children 22 months of age and older benefited from the presence of distal visual objects when searching for objects buried in a sandbox, whereas younger children did not (Newcombe et al., 1998). As allocentric spatial memory is a fundamental component of episodic memory, it is reasonable to theorize that children are unable to create episodic memories, complete with the experiential quality of reliving an episode in the locale where that episode took place (Piolino et al., 2008), before they can create allocentric spatial memories.

Another experiment by Ribordy et al. (2013) showed that the resolution of allocentric spatial memories acquired over repeated trials improves from 24 to 48 months of age. In the same open-field search task, children had to learn and remember three rewarded locations distributed among 18 potential locations. This task requires children to exhibit a high degree of spatial resolution ability in order to distinguish between adjacent locations (Bakker, Kirwan, Miller, & Stark, 2008; Gilbert, Kesner, & Lee, 2001). From 42 months of age, children were capable of discriminating locations above chance level (Ribordy et al., 2013). In a third experiment, the same authors tested children between 18- and 48-months of age over a 4-week period on a series of spatial tasks in which the distance between the potentially rewarded locations decreased, and the number of rewarded and potentially rewarded locations increased, from week to week (Ribordy Lambert et al., 2015). This experiment confirmed that allocentric spatial memory capacities improve from 2 to 4 years of age, and showed that children that failed at successive stages exhibited difficulty in discriminating locations that required high spatial resolution, also known as spatial pattern separation abilities, a process known to be subserved by the hippocampal formation (Bakker et al., 2008; Gilbert et al., 2001).

As described above, episodes occur once and only once. It is thus imperative that any information regarding an episode to be remembered for future recall be encoded without the benefit of repetition. It is thus possible that children's inability to form episodic memories incorporating allocentric spatial information arises from their inability to form allocentric spatial memories on a single-trial basis. In order to asses this possibility, we investigated the abilities of 3.5- to 7-year-old children to learn and remember allocentric spatial information on a single-trial basis. As each trial was temporally distinct, we were able to investigate the children's abilities to temporally resolve individual trials, that is, distinguish the current trial from the previous trial. We used the same open-field search task in which children older than 3.5 years of age exhibited high-resolution spatial abilities when given the opportunity to learn over repeated trials (Ribordy et al., 2013; Ribordy Lambert et al., 2015). In the present experiments, however, children had only one trial to learn the rewarded location(s). For each trial, children had to recall where they had last found the hidden rewards in a space that can only be defined using a high-precision allocentric representation. We describe the different manners in which single-trial, allocentric spatial memory performance improved for some children from 3.5 to 7 years of age, and how, for other children, performance did not improve with age.

2 | METHODS

2.1 | Participants

Participants were 40 children (27 males: 46–86 months; 13 females: 43–85 months) of primarily European descent and from middle-class families. Exclusion criteria were parent-reported neurological disorders (e.g., epilepsy) or developmental delays (e.g., children did not achieve typical developmental milestones such as walking or talking within the normal age range). Eighteen of the 40 children had participated in an earlier study (1–2 years prior) that investigated allocentric spatial memory capacities acquired over repeated trials (Ribordy et al., 2013). Their performance did not differ from that of participants who had not participated previously, and therefore data were grouped for analysis and presentation. Participants were tested during three sessions of approximately 45 min each, which generally took place once a week for three consecutive weeks. Testing took place Monday through Friday, between 8 A.M. and 6:30 P.M. Human subjects research was approved by the Intercantonal Ethics Committee for Jura, Neuchatel, Fribourg (protocol no. 10/2007), and the Ethical Commission for Clinical Research in Vaud (protocol no. 38/08), and was in accordance with the NIH guidelines for the use of human subjects in research. The participants' parents gave informed written consent.

Adult participants were 21 university students (10 males; 11 females; age range 20.58–32.21 years, average 23.18 years) of primarily European descent and from middle-class families, who received class credit for participation. Exclusion criteria were participant-reported neurological disorders (e.g., epilepsy). All adult participants gave

informed written consent. Adult participants' data have been previously published elsewhere (Banta Lavenex et al., 2015).

2.2 | Testing facility

We had testing facilities in two different locations: 21 children were tested in the canton of Vaud, and 19 in the canton of Fribourg. We found no differences in the behavior or performance of children tested in these two different locations, and therefore data were grouped for analysis and presentation. The main features of the testing facilities were consistent between the two sites. Testing took place within large rectangular rooms (Figure 1; Vaud: $9 \times 6\ m^2$; Fribourg: $7 \times 6\ m^2$) containing polarizing features such as doors, obscured windows, tables, chairs, wall posters. Within the room, a $4 \times 4\ m^2$ testing arena was created by making 3 walls of suspended, opaque fabric curtains. A rope delineated the front of the arena. Gaps at the front and the back created four entry points through which participants could enter and exit the arena (Figure 1). Entry order was determined pseudorandomly to preclude the use of egocentric strategies (Ribordy et al., 2013). Exterior to the two side walls, the visually distinct intertrial waiting areas contained two chairs with their backs to the arena. From within the arena, and from the intertrial waiting areas, participants had access to distant visual cues within the room. The floor was covered with uniform flooring so that no distinguishing marks could be used as landmarks. The testing arena was empty except for 18 white paper plates (18 cm in diameter) that were arranged in two concentric hexagons (Figure 1). An inverted opaque plastic cup (7.5 cm in diameter, 6.5 cm high) was placed on each plate. Food rewards could be hidden under the cups. All testing was videotaped with a video camera located in front of the arena.

2.3 | Procedure

Participants had to lift or turn over the plastic cups to obtain the hidden food reward. Rewards were usually Smarties®, Goldfish® crackers, pieces of breakfast cereal, or pretzels. All parents were queried with respect to alimentary allergies prior to testing. Children participated in three sessions on three different days (generally once a week for three consecutive weeks), with, respectively, 1, 2, or 3 rewarded locations (Figure 2). Each session consisted of 10 trials, and each trial presented new rewarded location(s). For the task with one rewarded location, no single location was rewarded twice: locations 14, 7, 13, 3, 16, 18, 1, 17, 9, and 15 were used sequentially. For the task with two rewarded locations, three of the locations were used twice (and location 13 was never used). For the task with three rewarded locations, all locations were used at least once, and 12 of the locations were used twice.

Each trial consisted of an encoding and a retrieval phase. Children first searched for the rewards when the rewarded location(s) were indicated by (a) red cup(s), whereas all non-rewarded (decoy) locations had white cups (Figure 2; encoding phase). Following a 1-min inter-phase interval, children searched for the rewards when all locations (rewarded and decoy locations) were covered by identical white cups (Figure 2; retrieval phase). Children could not discriminate these locations based on local features, but instead had to rely on an allocentric, spatial representation of the environment to discriminate these locations, that is, they needed to encode the goal locations in relation to distal environmental objects in the room.

All testing involved a team of two experimenters. Experimenter 1 (E1) would stay with the child throughout the testing session, enter the arena with the child, encourage the child to search for the rewards, praise the child when a reward was found, remove cups that had been searched, direct the child to the correct exit at the end of the trial, and occupy the child during the interphase and intertrial intervals by reading or talking. Experimenter 2 (E2) was responsible for replacing the rewards between trials, recording the data, and announcing the correct entry and exit doors. Accompanying adults that remained in the room were instructed not to say anything during the task. Both experimenters, and accompanying adults, wore dark sunglasses while the child was in the arena in order to avoid unintentionally cuing the child as to the locations of the rewards with eye gaze.

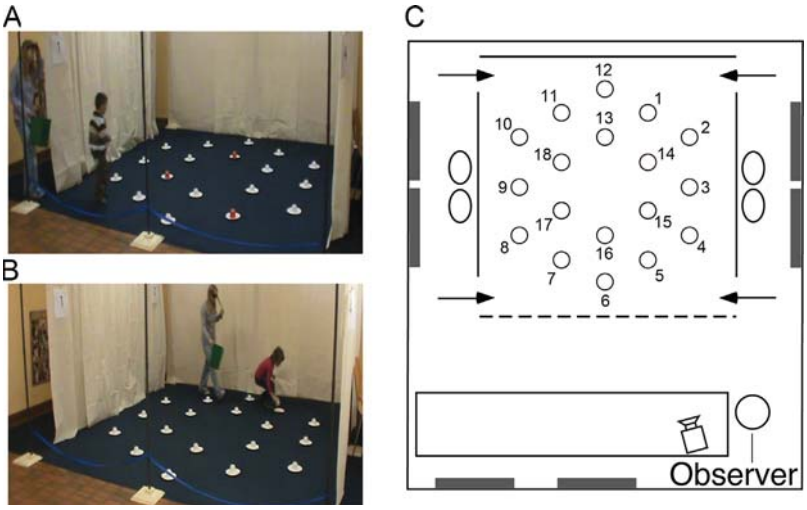

FIGURE 1 A. Picture of a participant in the arena in the encoding/local cue condition. B. Picture of a participant in the arena in the retrieval/allocentric spatial condition. C. Schematic of the testing room ($7 \times 6\ m^2$) and the arena ($4 \times 4\ m^2$), including tables, chairs, and posters/obscured windows/doors (gray rectangles)

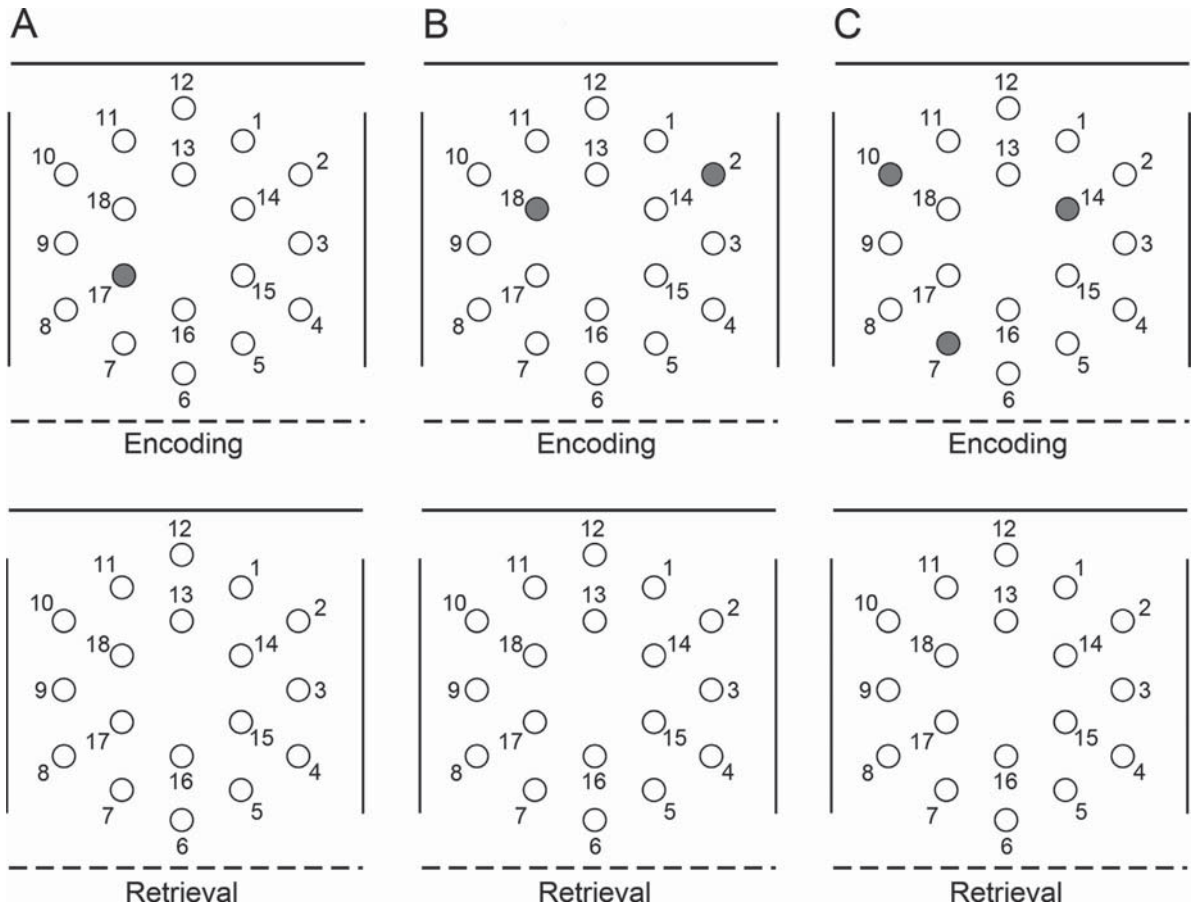

FIGURE 2 Examples of encoding and retrieval trials in the one location (A), two locations (B), or three locations (C) versions of the task

Before starting, E1 showed the child that treats could be hidden underneath cups. Upon entering the arena on the first encoding trial, E1 would explain to the child that if he looked under the cups he would find the place(s) that E2 had chosen for the treat(s). At this point, most children would either lift a red cup first, or lift a white cup first and, upon finding no reward, lift a red cup. Once a treat was found on the first encoding trial, and thereafter on all subsequent encoding trials, E1 would verbally praise the child. At the end of each encoding trial, E1 would then explain to the child that they should take one last careful look (at the now empty plates where red cups and rewards had been found) because the next time the child would come back into the arena, the treat(s) would be found in the same location(s), on the same plate(s). Upon entering the arena on subsequent encoding trials, E1 would prompt the child be saying "Let's see where E2 hid the treats this time."

Upon returning to the arena from a new entrance for the Retrieval phase (after the 1-min inter-phase interval), the child was reminded that the treats could be found at the same place as they had just found them. If, during the retrieval phase, children asked how many rewards remained to be found, E1 answered very explicitly, but without giving any indication about the rewarded locations ("Today there are always three treats. You already found two, so you have one more to find for this try"). If children wanted to lift other cups after having found all the rewards, E1 would tell the child that there were no more rewards to find during this specific trial, but that the child was allowed to search as many cups as desired. For children who did continue to search unrewarded locations, this behavior usually extinguished after one or two trials. Although children were given verbal encouragement and praise, they were never told or shown where the rewards were, or how to identify their locations. They were never told that when the red cups were present they could find the rewards there, nor were they verbally alerted to the spatial relations between objects in the room and reward locations. Although it may seem counterintuitive to not explain to the children that when red cups are present the rewards can be found underneath them, children of this age incorporate this information very quickly without explicit instruction. Thus, not explicitly telling the children that when red cups were present rewards could be found there did not seem to impact their understanding of the task or their performance.

2.4 | Data analysis

Statistical analyses were performed using SPSS 21. Regression analyses were performed to illustrate overall changes in performance in the Retrieval phase with age. We used General Linear Model analyses (GLMs) to compare the performance of different groups of children: we first separated the 40 children into two groups (20 younger vs. 20 older) based on a median split of age at 5.3 years

of age (young children: $M = 53.58$ mos, $SD = 6.4$ mos; old children: $M = 77.11$ mos, $SD = 6.39$ mos). For reasons explained in the Results Section, we split the older group into two subgroups: 10 children in the "old high-performing" group (5 girls; $M = 79.27$ mos, $SD = 6.18$ mos) consisted of older children whose performance, as evaluated by the number of correct choices before a first error, was at least 2 standard deviations above that of the younger children for at least one of the three memory load conditions (1, 2, or 3 rewarded locations). Ten other older children were in the "old low-performing" group (2 girls; $M = 74.96$ mos, $SD = 6.14$). There was no age difference between old low- and old high-performing children ($t_{(18)} = 1.565$, $p = .135$). GLM analyses were used to compare the performance of the young, old low- and old high-performing children groups, and between different memory loads (1, 2, and 3 locations). Unpaired t-tests were used to compare the performance of the group of old high-performing children with that of a group of adult individuals who participated in a previous experiment with one or three (but not two) goal locations (Banta Lavenex et al., 2015). Statistical significance was set at $p < .05$ for all analyses.

3 | RESULTS

3.1 | Overall performance

A regression analysis showed that the average number of locations that children needed to visit in the Retrival phase in order to find the rewarded locations across the three memory load conditions was related to age (total number visited [TNV] was normalized for the number of rewards in each condition; Figure 3A; TNV = 5.959–0.04 × age (in months), $R^2 = .34$, $F_{(1,38)} = 19.86$, $p < .001$). Similarly, the average number of correct choices children made before committing their first error was related to age (across memory loads; correct before error [CBE] was normalized for the number of rewards in each condition; Figure 3B; CBE = 0.077 + 0.005 × age (months), $R^2 = .15$, $F_{(1,38)} = 6.88$, $p < .02$). Finally, the average number of trials, across memory loads, in which children made no errors was also related to age (number of errorless trials [NET]; Figure 3C; NET = −0.258 + 0.051 × age (months), $R^2 = .18$, $F_{(1,38)} = 8.36$, $p < .001$). Thus, three different measures of task performance revealed that single-trial allocentric spatial memory performance improves with age. Although it may seem obvious that spatial memory performance should improve with age, it has been previously shown that children attain maximal performance on some allocentric spatial memory tasks acquired over repeated trials at 36 months of age (Ribordy Lambert et al., 2015). Thus, our finding that single-trial allocentric spatial learning improves between 43 and 86 months of age expands our knowledge concerning what types of learning and memory processes improve with age, and for how long these improvements persist during childhood.

Nevertheless, visual inspection of the scatter plots (Figure 3A–C) suggested that whereas performance among the younger children was rather homogeneous, performance among the older children was more heterogeneous. Indeed, although some older children exhibited performances substantially better than the younger children, the performance of many older children was not better. In order to investigate differences among older children in more detail, we further split the group of older children into two groups: Each child in the older "high-performing" group had a CBE score that was 2 standard deviations (*SD*) or more above the average CBE score of the younger group, in at least one of the three memory load conditions. Children in the "low-performing" group did not have any CBE score that was 2 *SD*s above the young cohort's average CBE score. We proceeded to compare the three groups of children (young, old high-performing, old low-performing) on the three measures of performance described above (CBE, TNV, and NET). It is critical to note that although the procedure that we used to designate the two groups of older children makes statistical comparisons between the old high-performing group

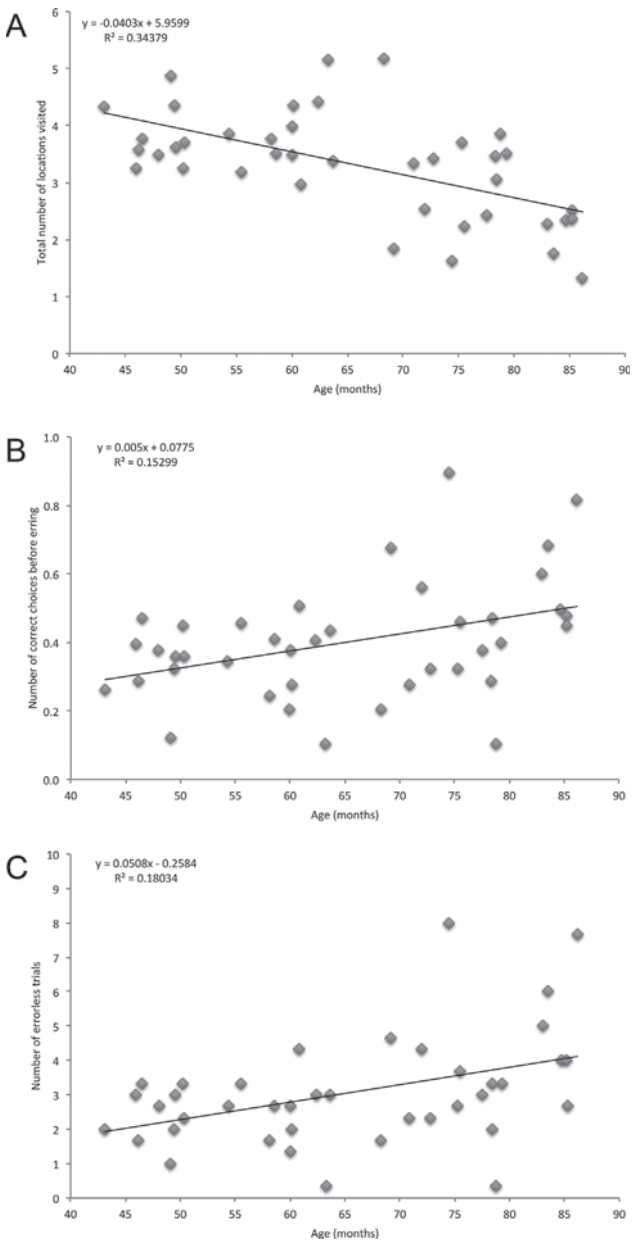

FIGURE 3 Individual performance across all three memory loads based on (A) the average number of locations visited to find all rewards (TNV; normalized for the number of rewards); (B) the average number of correct choices before erring (CBE; normalized for the number of rewards); and (C) the average number of errorless trials (NET)

and the young group meaningless, this procedure in no way invalidates statistical comparisons between either the old low- and old high-performing groups, nor between the old low-performing and the young groups of children. These comparisons are particularly revealing regarding which cognitive processes may be linked to improvements of performance with age.

3.2 | Single-trial spatial memory capacity: the influence of memory load

The number of correct choices children make in the Retrieval phase before committing their first error can be considered as a proxy for memory capacity: if children recall one location, but then fail to recall the second, their memory capacity can be considered to be one under those specific testing conditions. GLM analyses showed a main effect of age group (Figure 4; $F_{(2,\ 37)} = 23.055$, $p < .001$), an effect of memory load ($F_{(1.877,\ 69.452)} = 6.712$, $p = .003$; Mauchly's test of sphericity: Chi-square$_{(2)} = 6.803$, $p = .033$, Huynh–Feldt correction, Epsilon = .939), as well as an interaction between age group and memory load ($F_{(3.754,\ 69.452)} = 7.257$, $p < .001$). Old high-performing children made more correct choices before erring than old low-performing children (Fisher PLSD, $p < .05$). In contrast, and as suggested by the regression plots, the old low-performing group did not differ from the young group in the number of correct choices made before erring (Fisher PLSD, $p = .494$).

Close inspection of Figure 4 also shows that for old high-performing children, CBE increased between one and two locations (test of within-subjects contrasts: $F_{(1,9)} = 10.424$, $p = .010$), as should be expected if memory capacity is greater than 1. In contrast, CBE did not increase between two and three locations for this group, suggesting that memory capacity lies somewhere between two and three locations in this testing paradigm. For the young children, CBE did not vary from one, to two, to three locations ($F_{(1,19)} = 1.936$, $p = .180$), and remained around .5, as in the one location condition, suggesting that their memory capacity in this testing paradigm does not go above 1. Finally, the old low-performing group performed significantly worse with three locations than with one location ($F_{(1,9)} = 6.311$, $p = .033$), whereas their performance with two locations did not differ from that with one or three locations. This data suggest that old low-performing children behaved differently from both young and old high-performing children, and that their performance was more impaired at higher memory loads.

Interestingly, the old high-performing children's performance was close to that of adult university students tested on a similar paradigm (but with 23 rather than 18 potentially rewarded locations (Banta Lavenex et al., 2015)). Although, for one location the performance of the old high-performing children was less good than that of adults ($t_{(10.765)} = 2.850$, $p = .016$: Levene's test, $F_{(1,28)} = 25.519$, $p < .001$), it did not differ for three locations ($t_{(12.302)} = 1.620$, $p = .131$: Levene's test, $F_{(1,28)} = 5.548$, $p = .026$). Young adults were not tested with two locations.

Analyses of the total number of locations visited (TNV) and the number of errorless trials (NET) yielded very similar results: old high-performing children performed nearly as well as adults and outperformed the old low-performing children, and the performance of old low-performing children did not differ from that of young children (data not shown).

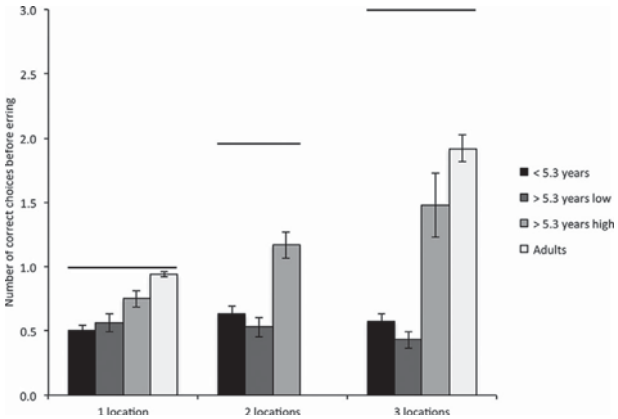

FIGURE 4 Number of correct goal locations visited before making an error, CBE, a proxy to estimate memory capacity. As indicated on the graph (solid horizontal lines above each set of bars), the maximum CBE is one for one location, two for two locations, and three for three locations

3.3 | Trial-by-trial variation in memory capacity: always a little, or sometimes a lot?

Because the CBE score is an average of correct choices across 10 trials, it is difficult to determine whether individuals, especially the young and low-performing older children, exhibited low but consistent memory capacity across trials, or if they chose two or three correct locations on some trials, but no correct locations on other trials. In order to answer this question, we analyzed the number of Retrival trials in which the first choice was correct (FCC). GLM analyses showed a main effect of age group ($F_{(2,\ 37)} = 16.539$, $p < .001$), an effect of memory load ($F_{(2,\ 74)} = 5.186$, $p = .008$; Mauchly's test of sphericity: Chi-square$_{(2)} = 4.089$, p =.129), but no significant interaction between age group and memory load ($F_{(4,\ 74)} = 1.530$, $p = .202$). Old high-performing children had more correct first choices than old low-performing children (Fisher PLSD, $p < .05$), and the number of correct first choices did not differ between the old low-performing and young children (Fisher PLSD, $p = .926$). Figure 5 shows that for both old

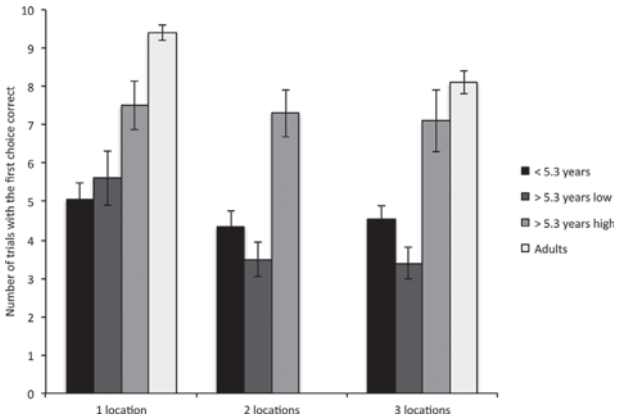

FIGURE 5 Number of trials with the first choice correct (FCC)

high-performing and young children, the number of first correct choices did not change with increasing memory load (tests of within-subjects contrasts; old high-performing: $F_{(1,9)} = .255$, $p = .625$; young; $F_{(1,19)} = 2.11$, $p = .163$). In contrast, old low-performing children made more first correct choices with one reward location than with two or three reward locations ($F_{(1,9)} = 14.716$, $p = .004$). Importantly, however, our analyses show that children were not guessing or making their first choices randomly. The probability to choose a rewarded location for the first choice by chance 3 out of 10 times (the lowest performance observed for all three groups of children across all three memory loads; Figure 5) is 0.017% for one location (1/18 × 1/18 × 1/18), 0.1% for two locations (2/18 × 2/18 × 2/18), and 0.5% for three locations (3/18 × 3/18 × 3/18).

The number of correct first choices made by old high-performing children was close to that of adult university students. Although, for one location the number of correct first choices made by the old high-performing group was slightly lower than that of adults ($t_{(10.765)} = 2.850$, $p = .016$: Levene's test, $F_{(1,28)} = 25.519$, $p < .001$), it did not differ for three locations ($t_{(11.361)} = 1.164$, $p = .268$: Levene's test, $F_{(1,28)} = 7.877$, $p = .009$).

3.4 | Analysis of errors: "where" versus "when"

Children were not instructed to retrieve the rewards in the same order that they had found them on the encoding phase since children of this age have great difficulty understanding ordinal concepts and the terms used to discuss them. Had we asked children to "Go to the first location first, the second location second," etc., age-dependent linguistic and conceptual competencies would have played a confounding role in task performance. Instead, we analyzed the first location chosen during retrieval in the two and three location conditions to determine whether children were sensitive to primacy or recency effects. Our analysis failed to reveal consistent effects of primacy or recency (data not shown).

In order to offer clues as to the cognitive processes contributing to improvements in performance, we analyzed the types of locations chosen when children made an error on their first choice upon entering the arena in the Retrival phase. Specifically, we analyzed whether incorrect first choices made with a memory load of 1 or 2, corresponded to: (1) the previous goal location(s) used in the immediately preceding trial, thus representing a difficulty in distinguishing between different trials, that is, a temporal resolution error; (2) locations adjacent to the goal location(s) (e.g., for location 5 [Figure 1], locations 6, 16, 15, and 4 are adjacent locations), thus representing a difficulty in distinguishing close locations, i.e., a spatial resolution error; or (3) other unrelated, random locations. Note that the numbers of different types of errors were normalized based on the probability to make those errors (i.e., divided by the number of locations in this category). We did not perform this analysis for three goal locations since an incorrect choice often belonged to two different categories, that is, a previous location was also an adjacent location, and incorrect locations could be adjacent to more than one goal location.

With one goal location (Figure 6), there was no main effect of age group ($F_{(2,36)} = .294$, $p = .747$), but a test of within-subjects contrasts revealed a main effect of choices ($F_{(1,36)} = 104.20$, $p < .001$) and a

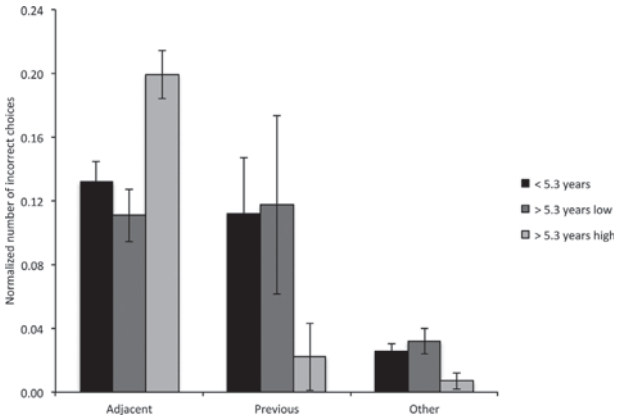

FIGURE 6 One location: analysis of errors for the first choice upon entering the arena. The three groups differed in the types of errors

choices by age group interaction ($F_{(2,36)} = 6.255$, $p = .005$). When erring, old high-performing children chose "Adjacent" locations more often than "Previous" and "Other" locations ($F_{(1,8)} = 86.820$, $p < .001$; Adjacent > Previous = Other). In contrast, when young children erred they chose "Previous" locations as often as "Adjacent" locations, and both more often than "Other" locations ($F_{(1,19)} = 38.65$, $p < .001$; Adjacent = Previous > Other). Revealingly, and similar to young children, old low-performing children also chose "Previous" locations as often as they did "Adjacent" locations ($F_{(1,9)} = 12.152$, $p = .007$; Adjacent = Previous, Adjacent > Other).

With two goal locations (Figure 7), there was no main effect of age group ($F_{(2,35)} = .296$, $p = .746$), but a test of within-subjects contrasts revealed a main effect of choices ($F_{(1,35)} = 152.11$, $p < .001$) and a choices by age group interaction ($F_{(2,35)} = 5.07$, $p = .012$). When old high-performing children erred, they chose "Adjacent" locations more often than "Previous" and "Other" locations ($F_{(1,7)} = 143.18$, $p < .001$; Adjacent > Previous = Other). When young children erred, they chose "Previous" locations as often as "Adjacent" locations, and both more often than "Other" locations ($F_{(1,19)} = 36.32$, $p < .001$; Adjacent = Previous > Other). Old low-performing children exhibited an error pattern that was intermediate between those of the old

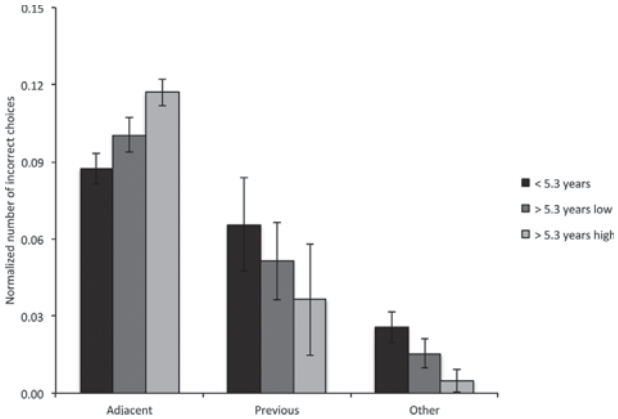

FIGURE 7 Two locations: analysis of errors for the first choice upon entering the arena. The three groups differed in the types of errors

high-performing and young children: They chose "Previous" locations less than "Adjacent" locations, but they still chose more "Previous" locations than "Other" locations ($F_{(1,9)} = 52.22$, $p < .001$; Adjacent > Previous > Other), meaning that although their rate of choosing "Previous" locations declined, it was still not equivalent to the decrease seen in the old high-performing children. This finding suggests that a gradual decrease in the number of "Previous" location errors contributes to the improvement of performance in this single-trial allocentric spatial memory task.

4 | DISCUSSION

Here, we investigated the abilities of 3.5- to 7-year-old children to learn and remember allocentric spatial information on a single-trial basis. For three measures of memory, CBE, TNV, and NET, performance improved with age. However, improvement across the age range tested here was not uniform: half of the children above 5.3 years of age performed nearly as well as 20–32-year-old adults, whereas the other half of the children above 5.3 years of age did not perform better than young children under 5.3 years of age. Children's improvements in single-trial learning and memory appeared to be linked to an increasing ability to spatially and temporally separate individual locations and events.

4.1 | Memory capacity

Although we found that single-trial allocentric spatial memory performance improved with age, our results confirmed that even the youngest children in our experiment (from 3.5 years of age) were capable of single-trial allocentric spatial learning. With one location, young children chose correctly on approximately one out of every two trials. Given that reliable discrimination of even one location in this paradigm requires high-resolution allocentric spatial processing (Banta Lavenex et al., 2014), and considering that children do not demonstrate proficiency at resolving such close locations until around 3.5 years of age (Ribordy Lambert et al., 2015), the performance of the young children in the condition with one location is impressive. Nevertheless, overall performance declined when these younger children were confronted with higher memory loads, with young children choosing correctly on only one of every four choices with two locations, and on only one of every six choices with three locations. This pattern of performance is to be contrasted with the ability of children of the same age to learn and remember the position of three-rewarded locations in the same open-field paradigm when given the opportunity to learn over repeated trials (20 trials over 2 days (Ribordy et al., 2013)).

However, whereas the CBE measure shows declining performance with increasing memory load in the youngest children, examination of the number of first correct choices they made presents a different picture: young children chose a correct location for their first choice on about 50% of the trials regardless of whether there were one, two, or three locations to be remembered. This suggests that when two or three locations were presented simultaneously, children could encode, store and recall at least one location, but not more than one location reliably. In contrast to the youngest children's ability to recall one location was the relatively poor performance of the old low-performing children. Indeed, children in this group made fewer correct first choices when there were two or three locations to be remembered than when there was only one, exhibiting a negative impact of memory load.

For the old high-performing children, their performance with one location was slightly less good than that of adults. In contrast, their performance was not different from that of adults when tested with three locations, a task a priori more difficult (*NB:* adults were not tested with two locations). The fact that old high-performing children performed slightly more poorly than adults with one location, but not three, could ostensibly be due to a slower learning of the task's rules (i.e., the fact that it is the red cup that hides the reward in the first trial must be learned incidentally). However, for the first trial, our analyses show that 6 of the 10 old high-performing children chose correctly the red cup for their first choice in the encoding phase, and then chose the correct spatial location during the recall phase. The other four old high-performing children incorrectly chose a white cup for their first choice during the encoding phase, but then all chose the correct spatial location for their first choice during the recall phase. Thus, it seems unlikely that the poorer performance of these children in the one location task was due to poorer learning of the task. Instead, we can hypothesize that either the demands of the task were too low for some of the individuals in this group, who thus allocated minimal resources to performing optimally, and thus occasionally made some errors of inattention. For the two and three location tasks, the increased task difficulty may have increased the children's motivation and thus their attention/concentration (the Yerkes–Dodson effect). Alternatively, or perhaps in addition, it might be that although the task was equally simple for adult participants, social-psychological influences on performance (such as the audience effect and/or their desire to please the experimenter with perfect performance) may have served to elicit improved performance in the one location task for this group. In any case, the small performance differences observed between the old high-performing children and the adults do not appear to be due to fundamental differences in memory processes, but rather small variations due to attention and/or motivation.

Although the differences between the old low- and high-performing groups are striking, we believe that we have just caught a snapshot of the old low-performing individuals at a certain stage of development. Indeed, such low levels of performance are not seen in adult participants (coming from a wide variety of socio-economic and educational backgrounds; (Banta Lavenex et al., 2014, 2015)). It is, therefore, reasonable to assume that these children are still developing, and their allocentric short-term memory processes will soon improve to match the level of their high-performing peers. We can conclude that although from 5 years of age some children exhibit adult-like, single-trial allocentric spatial memory capacities, significant individual differences still exist at this age.

4.2 | Encoding precision

In our task, children could make three different types of errors: (1) spatial precision errors indicated by the choice of a location adjacent to

the rewarded location; (2) temporal precision errors indicated by the choice of a location rewarded on the preceding trial; and (3) “Other” errors indicated by the choice of a location neither adjacent to the reward, nor rewarded on the preceding trial. “Other” errors may signify children's memory failures, either false memories of the rewarded location, or random guesses when the child had no idea where they had previously seen the reward. Critical to understanding children's memory abilities is the fact that they made very few “Other” errors, suggesting that children did not experience memory failures. Instead, the vast majority of errors were associated with imprecisions in the resolution of either spatial or temporal coding.

4.2.1 | Spatial resolution

It has been proposed that gradual improvements in spatial resolution and allocentric spatial memory performance in children from 24 to 48 months are subserved by improvements in spatial pattern separation abilities (Ribordy Lambert et al., 2015). Although gross topographic allocentric coding seems to emerge around 2 years of age and remains available in order to solve basic allocentric tasks across the lifespan (Newcombe et al., 1998; Ribordy et al., 2013), as children age they become more competent at using angular and distance information to determine the precise coordinates of locations in allocentric terms. These findings are consistent with the model of Huttenlocher and co-workers who described spatial processing as consisting of a categorical spatial system and a fine-grained spatial system (Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Newcombe, & Sandberg, 1994). Interestingly, a pioneering study by Acredolo, Pick, and Olsen (1975) found that 8-year-old children showed greater precision in remembering where an item had been dropped than 3- and 4-year-old children; they hypothesized that age-related improvements were due to an increasing ability to use metric information to code locations.

In the current study, 5–7-year-old high-performing children performed nearly as well as adults, suggesting that their allocentric spatial capacities are almost adult-like. Nonetheless, as described above, old high-performing children still made more errors in the one location task than adults. The vast majority of errors that old high-performing children made were choices of adjacent non-rewarded locations, that is, errors in spatial precision. Similarly, a large proportion of errors that both young and old low-performing children made were also due to errors in spatial precision (“Adjacent” choices). These findings provide further evidence that improvements in spatial resolution abilities in children contribute to improvements in allocentric spatial memory performance.

4.2.2 | Temporal resolution

There is a relatively large literature concerning the temporal coding of children's event memories. Briefly, whereas children as young as 4 years of age are capable of distinguishing between relatively recent and less recent events (i.e., making temporal distance judgments (Friedman, 1991)), children even up to 8 years of age have difficulty in temporally sequencing individual instances of a repeated event (compared to one-time events (Roberts et al., 2015)). Nevertheless, and similar to spatial memory, children's temporal coding of unique events improves between 3 and 8 years of age (Drummey & Newcombe, 2002; Hayne & Imuta, 2011).

In the current study, decreases in temporal resolution errors are associated with age-dependent improvements in single-trial, allocentric spatial learning and memory performance: young children often chose locations that had been rewarded on the preceding trial when erring, whereas old high-performing children seldom choose previously rewarded locations when erring. Importantly, old low-performing children exhibited an intermediate performance, making many more temporal resolution errors than old high-performing children. Our findings are thus consistent with those of (Roberts et al., 2015) concerning the impairments that young children have in forming clear memory representations of repeated events, but further suggest that these difficulties arise during encoding or the earliest stages of consolidation, as our task's intertrial interval was a few minutes rather than hours or days.

4.3 | Memory precision predicts memory capacity

Memory capacity is generally inferred from the number of correct responses that a participant provides. In our study, the young and low-performing older children did not exhibit impressive memory capacities, recalling at most only one location per trial. However, the majority of their errors made on the first choice were either errors in spatial or temporal resolution. It has been previously shown in adults that memory precision can predict memory capacity for spatial and non-spatial information (Banta Lavenex et al., 2015), and we propose that this is also the case for children. Specifically, because the majority of the young children's errors were either spatial or temporal resolution errors, this suggests that children either remembered the general area of the rewarded location, or remembered a previously rewarded location from the preceding trial. Thus, for the children in our study, it may not be that memory capacity per se was poor, but rather memory precision. If their spatial and/or temporal coding had been more precise, their demonstrated memory capacity may have been greater, supporting further the link between precision and capacity.

Finally, it is worth noting that many of the studies which investigate memory capacity in children implement paradigms in which children must not only recall which items they have seen, but also the order in which they were seen (Alloway, Gathercole, & Pickering, 2006; Barrouillet & Camos, 2001; Bertrand & Camos, 2015). Interestingly, such studies have similarly shown a shift in performance between 4 and 7 years of age. Considering the findings from the current study, in combination with those of previous studies, it is appropriate to wonder whether some of the limits on memory capacity observed in children of this age may be attributed to imprecise temporal coding, thus limiting the memory capacity that can be demonstrated.

4.4 | Deconstructing episodic memory to define the developmental trajectories of the individual components

Recent studies of episodic memory have designed paradigms to tease apart or deconstruct episodic memories acquired via

experimenter-defined events in order to analyze "what," "where," and "when" components independently. For example, Hayne and Imuta (2011) went to the homes of 3- and 4-year-old children and hid three different toys in three different locations (e.g., under a bed, behind a couch), in three different rooms. Following a 5-min retention interval, 3- and 4-year-old children exhibited the best recall for the room where the object was hidden, but recalled the temporal order of hiding less well. Although our results are largely coherent with these findings, in our study we found that 3- and 4-year-old children made spatial and temporal errors with approximately equal frequency. This difference in the apparent development of spatial versus temporal coding may be explained by the fact that in the Hayne and Imuta (2011) study, children could benefit from being tested in a familiar environment, and in which hiding locations were unique (e.g., only one couch, only one parent's bed, etc.) and could be labeled semantically, thus likely favoring improved spatial as compared to temporal encoding.

Bauer et al. (2012) investigated whether 4-, 6-, and 8-year-old children could remember "which event" occurred "where" inside an experimental room. After a substantial 7-day retention interval (range 6–14 days), all three groups of children were significantly worse at recalling both the event and its location, as compared to either the event or the location alone. Specifically, the probability that children successfully reported where a specific event took place was only 25% for 4-year olds, 40% for 6-year olds, and 60% for 8-year olds. Overall, and similar to our findings, these results indicate significant improvement in children's memory for the locations at which they experienced specific events from 4 to 8 years of age (Bauer et al., 2012).

In another study, Newcombe et al. (2014) investigated whether 15–56-month-old children could remember where, in which context/room, they found a hidden toy. As four containers were available to be searched, Newcombe and co-workers set their criteria for random search behavior at 25%, and concluded that children 34 months of age and older performed the task above chance level, presumably by binding the room context with the container to be searched in that room. However, considering the representational demands needed to solve their task (Banta Lavenex & Lavenex, 2015; Eichenbaum, Fagan, Mathews, & Cohen, 1988), as only two of the four containers ever hid the toys (the cylinder in the Rainbow room and the box in the Cloud Castle room) children needed only to remember the identity of the two containers, independent of the room context, in order to make 50% correct searches, which would be statistically significant based on their criteria of 25% chance. Examining their results from this perspective, only children 42 months of age and older performed above 50% chance (Newcombe et al., 2014; Figure 4) and thus exhibited evidence of specific contextual coding in this trial-unique episodic-like memory task. These results are in agreement with our current findings showing that children from 3.5 years of age are capable of single-trial learning of high-resolution spatial information.

Other studies have taken the approach of analyzing the developmental trajectories of the "what," "where," or "when" components separately, and thus independently of episodic events, in order to identify age-specific deficiencies in the individual components fundamental for constructing episodic memories (Lee et al., 2016; Ribordy et al., 2013; Ribordy Lambert et al., 2015). For example, a recent study by Lee et al. (2016) compared 8–11-year-old children's abilities to remember item–space, item–time, and item–item relations, in order to evaluate the development of presumably hippocampal dependent-binding processes: that is, the building blocks of episodic memory. The authors reported differential developmental trajectories, with item–space memory mostly mature in 8-year olds, and item–space performance better than item-time performance across all ages, and finally, item–item memory showing the lowest performance levels and being the slowest to mature. Considering the representational demands necessary to solve their task, however, it is likely that they did not assess hippocampal-dependent binding. For example, for their item-space task, because their stimuli are presented on the screen directly in front of the seated participant, non-hippocampal processes can be used to encode the location of the stimuli (e.g., egocentric representations relying on retinotopic or parietal coding). Similarly, because the stimuli in their item-time task are presented sequentially, and thus never necessarily required to be "associated" or "bound" to any given event or object, simple associations between the visual item and a semanticized ordinal position (e.g., 1, 2, 3; Lee et al., 2016) may have sufficed to code temporal order, a process which may be accomplished extra-hippocampally. Indeed, only their item–item task where participants had to determine if three obscure items, of a total of nine obscure items shown, had been shown simultaneously, is likely hippocampal dependent. Not surprisingly, performance on this task was the worst across all age groups, and exhibited the slowest developmental time course. In sum, whereas the authors aimed to study the building blocks of episodic, hippocampus-dependent memory, an assessment of the representational demands necessary to solve two of their three tasks suggests that hippocampal involvement is unnecessary, thus making the developmental timelines that they proposed likely inappropriate for extrapolating to episodic memory.

In the present study, children were asked to learn and remember reward locations that could only be encoded using high resolution allocentric spatial processes, known to depend on the hippocampal formation (Banta Lavenex et al., 2014; Kolarik et al., 2016). Moreover, children had to associate/bind the locations seen during each trial into a temporal episode, distinct from the preceding trial(s), a process also believed to depend on the hippocampal formation (Eichenbaum, 2014). Children did not make random errors, but rather made errors in either spatial or temporal resolution. Furthermore, children's temporal precision seemed to mature earlier than their spatial precision, findings which are consistent with Bauer's (Bauer et al., 2012) showing the protracted development of event-location binding. Whereas Lee et al. (2016) attributed poor performance to immature hippocampal binding processes in general, our results lead to a slightly different hypothesis: the errors that we observed in children's spatial and temporal resolution suggest that this information is highly susceptible to interference from close spatial and temporal content. Evidence suggests that these types of temporal and spatial resolution errors may result specifically from impaired hippocampus-dependent pattern separation processes (Bakker et al., 2008; Gilbert et al., 2001).

5 | CONCLUSION

In sum, our findings suggests that increases in both allocentric spatial memory precision and temporal precision underlie improvements in single-trial allocentric spatial memory capacity seen in children from 3.5 to 7 years of age. These same improvements in allocentric spatial and temporal memory precision may also underlie improvements in the ability of children to successfully encode detailed information about specific episodes, in particular information about "where" and "when" sequential events took place.

ACKNOWLEDGMENTS

The authors would like to thank all of the children and their families for their participation. This research was supported by the Swiss National Science Foundation: grants PMPDP3-122844 and PMPDP3-128996 to PBL. The Swiss National Science Foundation had no involvement in the study design, nor in the collection, analysis or interpretation of the data, nor in the writing of this report or the decision to submit it for publication.

Disclosure: The authors have no conflicts of interest to declare.

REFERENCES

Acredolo, L. P., Pick, H. L., & Olsen, M. G. (1975). Environmental differentiation and familiarity as determinants of children's memory for spatial location. *Developmental Psychology*, *11*, 495–501.

Alloway, T. P., Gathercole, S. E., & Pickering, S. J. (2006). Verbal and visuospatial short-term and working memory in children: Are they separable? *Child Development*, *77*, 1698–1716. DOI: 10.1111/j.1467-8624.2006.00968.x17107455

Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. (2008). Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science*, *319*, 1640–1642. DOI: 10.1126/science.1152882

Banta Lavenex, P., Boujon, V., Ndarugendamwo, A., & Lavenex, P. (2015). Human short-term spatial memory: Precision predicts capacity. *Cognitive Psychology*, *77*, 1–19.

Banta Lavenex, P., Colombo, F., Ribordy Lambert, F., & Lavenex, P. (2014). The human hippocampus beyond the cognitive map: Evidence from a densely amnesic patient. *Frontiers in Human Neuroscience*, 1–18. DOI: 10.3389/fnhum.2014.00711

Banta Lavenex, P., & Lavenex, P. (2015). The ontogeny of human memory: Where are we going? *International Journal of Behavioral Development*, *39*, 308–309.

Barrouillet, P., & Camos, V. (2001). Developmental increase in working memory span: Resource sharing or temporal decay? *Journal of Memory and Language*, *45*, 1–20.

Bauer, P. J. (2007). *Remembering the times of our lives: Memory in infancy and beyond. The Developing Mind Series* (p. 437). New York: Psychology Press.

Bauer, P. J., Doydum, A. O., Pathman, T., Larkina, M., Guler, O. E., & Burch, M. (2012). It's all about location, location, location: Children's memory for the "where" of personally experienced events. *Journal of Experimental Child Psychology*, *113*, 510–522. DOI: 10.1016/j.jecp.2012.06.00723010356

Bertrand, R., & Camos, V. (2015). The role of attention in preschoolers' working memory. *Cognitive Development*, *33*, 14–27. DOI: 10.1016/J.Cogdev.2014.10.002

Burgess, N. (2002). The hippocampus, space, and viewpoints in episodic memory. *Quarterly Journal of Experimental Psychology A*, *55*, 1057–1080. DOI: 10.1080/02724980244000224

Drummey, A. B., & Newcombe, N. S. (2002). Developmental changes in source memory. *Developmental Science*, *5*, 502–513.

Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*, 732–744. DOI: 10.1038/nrn3827

Eichenbaum, H., Fagan, A., Mathews, P., & Cohen, N. J. (1988). Hippocampal system dysfunction and odor discrimination learning in rats: Impairment or facilitation depending on representational demands. *Behavioral Neuroscience*, *102*, 331–339.

Friedman, W. J. (1991). The development of children's memory for the time of past events. *Child Development*, *62*, 139–155. DOI: 10.2307/1130710

Gilbert, P. E., Kesner, R. P., & Lee, I. (2001). Dissociating hippocampal subregions: Double dissociation between dentate gyrus and CA1. *Hippocampus*, *11*, 626–636. DOI: 10.1002/hipo.1077

Hayne, H., & Imuta, K. (2011). Episodic memory in 3-and 4-year-old children. *Developmental Psychobiology*, *53*, 317–322.

Hoscheidt, S. M., Nadel, L., Payne, J., & Ryan, L. (2010). Hippocampal activation during retrieval of spatial context from episodic and semantic memory. *Behavioural Brain Research*, *212*, 121–132. DOI: 10.1016.j.bbr.2010.04.010

Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, *98*, 352–376.

Huttenlocher, J., Newcombe, N., & Sandberg, E. H. (1994). The coding of spatial location in young children. *Cognitive Psychology*, *27*, 115–147.

Jack, F., & Hayne, H. (2010). Childhood amnesia: Empirical evidence for a two-stage phenomenon. *Memory*, *18*, 831–844. DOI: 10.1080/09658211.2010.51047620924948

Kolarik, B. S., Shahlaie, K., Hassan, A., Borders, A. A., Kaufman, K. C., Gurkoff, G., . . . Ekstrom, A. D. (2016). Impairments in precision, rather than spatial strategy, characterize performance on the virtual Morris water maze: A case study. *Neuropsychologia*,, *80*, 90–101. DOI: 10.1016/j.neuropsychologia.2015.11.013

Lavenex, P., & Banta Lavenex, P. (2013). Building hippocampal circuits to learn and remember: Insights into the development of human memory. *Behavioural Brain Research*, *254*, 8–21. DOI: 10.1016/j.bbr.2013.02.007

Lee, J. K., Wendelken, C., Bunge, S. A., & Ghetti, S. (2016). A time and place for everything: Developmental differences in the building blocks of episodic memory. *Child Development*, *87*, 194–210. DOI: 10.1111/cdev.12447

Newcombe, N. S., Balcomb, F., Ferrara, K., Hansen, M., & Koski, J. (2014). Two rooms, two representations? Episodic-like memory in toddlers and preschoolers. *Developmental Science*, *17*, 743–756. DOI: 10.1111/desc.12162

Newcombe, N. S., Huttenlocher, J., Bullock Drummey, A., & Wiley, J. G. (1998). The development of spatial coding: Place learning and dead reckoning in the second and third years. *Cognitive Development*, *13*, 185–200.

Newcombe, N. S., Lloyd, M. E., & Ratliff, K. R., (2007). Development of episodic and autobiographical memory: A cognitive neuroscience perspective. In V. Kail (Ed.), *Advances in child development and behavior* (p. 426). San Diego, CA: Elsevier, vol. *35*.

Nyberg, L., McIntosh, A. R., Cabeza, R., Habib, R., Houle, S., & Tulving, E. (1996). General and specific brain regions involved in encoding and retrieval of events: What, where, and when. *Proceedings of the National Academy of Sciences USA*, *93*, 11280–11285.

Piolino, P., Desgranges, B., Hubert, V., Bernard, F. A., Matuszewski, V., Chetelat, G., ... Eustache, F. (2008). Reliving lifelong episodic autobiographical memories via the hippocampus: A correlative resting PET study in healthy middle-aged subjects. *Hippocampus*, *18*, 445–459. DOI: 10.1002/hipo.20406

Ribordy, F., Jabes, A., Banta Lavenex, P., & Lavenex, P. (2013). Development of allocentric spatial memory abilities in children from 18 months to 5 years of age. *Cognitive Psychology*, *66*, 1–29. DOI: 10.1016/j.cogpsych.2012.08.001

Ribordy Lambert, F., Lavenex, P., & Banta Lavenex, P. (2015). Improvement of allocentric spatial memory resolution in children from 2 to 4 years of age. *International Journal of Behavioral Development*, *39*, 318–331.

Roberts, K. P., Brubacher, S. P., Drohan-Jennings, D., Glisic, U., Powell, M. B., & Friedman, W. J. (2015). Developmental differences in the ability to provide temporal information about repeated events. *Applied Cognitive Psychology*, *29*, 407–417. DOI: 10.1002/acp.3118

Rubin, D. C. (2000). The distribution of early childhood memories. *Memory*, *8*, 265–269.

Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I. A., & Evans, S. (2002). Single-trial learning of "what" and "who" information in a gorilla (Gorilla gorilla gorilla): implications for episodic memory. *Animal Cognition*, *5*, 85–90. DOI: 10.1007/s10071-002-0132-0

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, *20*, 11–21.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25.

Zola-Morgan, S., Squire, L. R., & Amaral, D. G. (1986). Human amnesia and the medial temporal region enduring memory impairment following a bilateral lesion limited to field CA1 of the hippocampus. *Journal of Neuroscience*, *6*, 2950–2967.